

While the wolf is away: Modelling the dynamics of a moose population in a protected area

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ABSTRACT

High-density populations can threaten the ecological integrity of ecosystems through cascading effects. In such cases, management practices must be guided by sufficient knowledge of the biological mechanisms at play. Simulation models are powerful tools for acquiring such knowledge. The moose (*Alces alces americana*) is a species that recently became overabundant in some areas of eastern North America, sometimes requiring specific management measures. While numerous models exist for moose population dynamics, few are adapted to high density populations like the one in Forillon National Park (Quebec, Canada), a protected area in which the moose's apical predator (grey wolf *Canis lupus*) is absent. We developed a sex- and age-structured population model respecting these conditions that we parameterized using pattern-oriented modelling to help explain the changes in moose density observed over nearly 4 decades. The most plausible sequence of vital rates identified exhibited negative density dependence in survival, reproduction and dispersal. Predation by alternative predators, black bears (*Ursus americanus*) and coyotes (*Canis latrans*), caused substantial mortality of calves each year. Unlike elsewhere in northeastern North America, winter tick only had a slight effect on calf survival. Variations in the population's sex ratio were mainly explained by sex-biased dispersal. Our study provides new insights concerning the dynamics of high-density ungulate populations in the absence of their apical predator, and our modelling approach helped reveal new methodological challenges and opportunities. We also present a comprehensive process to build and parameterize a complex population model using scarce data.

1. Introduction

Year-to-year fluctuations of abundance are common in wild-ranging animal populations. A variety of intrinsic and extrinsic factors (hereafter called “dynamics-driving factors”; e.g. competition, predation, human activities, climate, disease) are likely to affect the vital rates (i.e. survival, recruitment and dispersal) that influence a population's size over time (Nicholson, 1933; Turchin, 2003; Rushing et al., 2017). How these factors can limit vital rates is a constant subject of research in population ecology, since their interactions are not yet fully understood (Sutherland et al., 2013; Krebs, 2020).

The carrying capacity is the maximum number of individuals that can be sustained by an ecosystem for a given species (Pearl and Reed, 1920; MacNab, 1985). Some populations are maintained well below this number by the combined effect of several dynamics-driving factors,

which may even cause their decline (e.g. woodland caribou *Rangifer tarandus caribou*: Wittmer et al., 2005; wild salmon *Oncorhynchus* spp.: Miller et al., 2014). These low-density populations are of particular concern for population ecologists, as conservation issues are crucial in a context of biodiversity crisis.

However, in other cases, the relaxation of one or more of the dynamics-driving factors can trigger a population growth toward higher densities nearing the carrying capacity (e.g. eastern grey kangaroo *Macropus giganteus*: Banks et al., 2000; moose *Alces alces*: Dzikowski-Michalska et al., 2019). These high-density populations should also be carefully considered, as they have the potential to cause a variety of problems, such as the transmission of diseases to humans (raccoon *Procyon lotor*: Majeau et al., 2023), the extirpation of prey populations (red fox *Vulpes vulpes*: Kinnear et al., 2002) and a change in the vegetation structure (sika deer *Cervus nippon*: Nishizawa et al., 2016). They

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can irreversibly alter the community structure via cascading effects and result in a completely different ecosystem (Côté et al., 2004; Dexter et al., 2013). Thus, government agencies and land managers may want to control certain populations to preserve the ecosystem's ecological integrity (Mills et al., 2020; Valente et al., 2020). To be effective, such interventions must be based on a sufficient understanding—and empirical evidence—of the mechanisms that drive the dynamics of the focal populations (Leopold, 1933; Jean, 1998; Mills and Johnson, 2013). Gathering relevant data and building such knowledge can require extensive field sampling and surveys as well as important investments in time and money (Noyes et al., 2000; Environmental Protection Authority, 2020). Hence, wildlife and land-use managers and policy-makers sometimes rely on simulation models to overcome these difficulties (Jean, 1998; McLane et al., 2011; Niemuth et al., 2021), especially when data are scarce.

Models are synthetical and quantitative tools that are especially helpful in population ecology (Akçakaya et al., 1999; McLane et al., 2011). They are precious allies to understand and explain the causal mechanisms of population dynamics (Jean, 1998; White, 2000). Sex- or age-structured models are among the most frequently used, since they fit with the life-history traits of many animal species (Jensen, 2000; Mignatti et al., 2012; Winker et al., 2020). Through their separate treatment of different classes of individuals, these models help to assess the relative importance of demographic drivers in shaping population dynamics and to adapt management practices.

The moose is a very important game species of great economic and cultural interest throughout its distribution range (Timmermann and Rodgers, 2005; Lefort and Massé, 2015). While a decline in moose populations is currently observed in some areas of North America (e.g. Alberta, Idaho, New Hampshire, Ontario, Newfoundland: Timmermann and Rodgers, 2017; Manitoba, Saskatchewan: Arsenault et al., 2019), elsewhere, densities have been reported to increase over the last decade (Alaska, Maine, New Brunswick: Timmermann and Rodgers, 2017; Quebec: Lefort and Massé, 2015; Desgagnés et al., 2022), potentially causing lasting damage to the forest areas moose inhabit (Rotter and Rebertus, 2015; De Vriendt et al., 2021). Therefore, it appears essential to closely monitor high-density moose populations and identify the factors at play (McLaren et al., 2004; Valente et al., 2020).

Messier (1991) analyzed the contribution of food competition, wolf (*Canis lupus*) predation and snow accumulation to the interannual variation of moose abundance on Isle Royale (northeastern US). His results suggest that moose population dynamics in this area are led by food competition (triggering a population decline at high densities) and wolf predation (being regulatory at low densities and antiregulatory at high densities). Indeed, an impressive increase in moose abundance was observed after a wolf population decline on this island between 1980 and 1996, followed by a massive moose population crash due to starvation (Peterson, 1999). In other sectors where predation was low, the moose populations kept growing for several years despite high harvest densities or low pregnancy and twinning rates resulting from negative density dependence (White et al., 2006; Boertje et al., 2009). In Poland, the “top-down control” exerted by wolves on a moose population was surpassed by the interplay of a ban on culling, the proximity of preferred habitats, and a sex ratio severely skewed toward females, which promoted reproductive success (Dziki-Michalska et al., 2019). Similarly, a rapid increase in moose numbers occurred in the 1970s in Fennoscandia due to the combination of a shift in forest management practices (creating large areas of highly suitable forage for moose), favourable sex- and age-specific harvesting and very low predation by wolves and bears (Lavsund et al., 2003). In the Matane Wildlife Reserve (eastern Canada), where the wolf has been extirpated for more than 150 years, the moose population maintained its growth rate even at a density of 3 moose/km² by reducing the twinning ovulation rate, thus ensuring a higher probability to reproduce from year to year (Gingras et al., 2014).

Among the studies conducted on high-density moose populations, very few took place in the absence of both of the two main causes of

mortality: the grey wolf, the apical predator of moose, and hunting (but see McLaren et al., 2000). Consequently, we have few tools to understand which drivers shape the population dynamics of this cervid species under such circumstances, but some interesting results obtained for another ungulate species can be used as a starting point. For instance, Hebblewhite et al. (2002) reported that elk (*Cervus elaphus*) population growth was driven by density and human-caused mortality (highway and railway) in Banff National Park in the quasi absence of wolf predation. Lubow et al. (2002) modeled the size of an elk subpopulation of the Rocky Mountain National Park in winter between 1965 and 2001 and noticed that the vital rates were not significantly influenced by winter temperature or by summer temperature or precipitation but showed important evidence of density dependence.

In this study, we aimed at improving our understanding of the dynamics of high-density moose populations living in a protected area where no sport harvest or logging is allowed, and where the main predator has been absent for over 150 years. To do so, we built a sex- and age-structured population model to identify the factors—and their interactions—that drove the dynamics of a high-density moose population living in a protected area with such conditions over nearly 4 decades. We hypothesized that in this system, climate, intraspecific competition and parasitism would explain most of the fluctuations in moose population size, and that their relative influence would vary over time and according to the density of the population. We aim to provide new information about the biological mechanisms at play for ungulate populations in protected areas in the absence of their apical predator, which should be accounted for by managers for conservation planning. Our study also presents a comprehensive description of the process of building a complex population model and parameterizing it when only scarce data are available.

2. Methods

2.1. Study area

Our study area covers the Forillon National Park, located at the tip of the Gaspé Peninsula in Quebec (Canada), and some adjacent areas (Fig. 1a). Delimited by the Gulf of St. Lawrence, the Gaspé Bay and Highway 197, the 245 km² study area can be considered as geographically closed by these natural barriers (water bodies) coupled with the recent urban development along Highway 197, which constrains animal emigration and immigration (Pettigrew et al., 2021). Logging is forbidden in the park since its creation in 1970, and hunting can only occur on the adjacent private and public lands since then. Highway 132 passes in the Forillon National Park along the coast, and the park territory supports several hiking and cross-country skiing trails.

Elevation ranges from 0 to 560 m a.s.l., and the landscape is a complex mosaic of valleys, ravines, mountains, streams and a few lakes (Lafleur, 1972). The study area experiences a humid continental climate with several days of strong winds and fog (Robitaille and Saucier, 1998). From 1982 to 2020, temperatures ranged between -35.5°C and +36.0°C, the mean annual precipitation reached up to 752 mm of rain and the mean annual snowfall was of 375 cm between mid-November and late April (maximum snow depth of 244 cm) (Environment and Climate Change Canada, 2021). The forested area is representative of the balsam fir (*Abies balsamea*) – yellow birch (*Betula alleghaniensis*) bioclimatic domain and covers most (95 %) of the park. Some old, abandoned fields complete land covers (Comeau et al., 2006; Brandt, 2009). Tree cover in the valleys primarily consists of yellow birch and maple (*Acer* spp.), while lowlands are occupied by balsam fir and yellow birch, along with northern white cedar (*Thuja occidentalis*) in wet areas. Highlands are dominated by balsam fir, white birch (*B. papyrifera*) and white spruce (*Picea glauca*) (Majcen, 1974). A large part (~70 %) of the coniferous stands within the park limits was affected by a spruce budworm (*Choristoneura fumiferana*) outbreak between 1975 and 1992 (Boulanger and Arsenault, 2004), converting an area (< 4 % of the park's surface) into

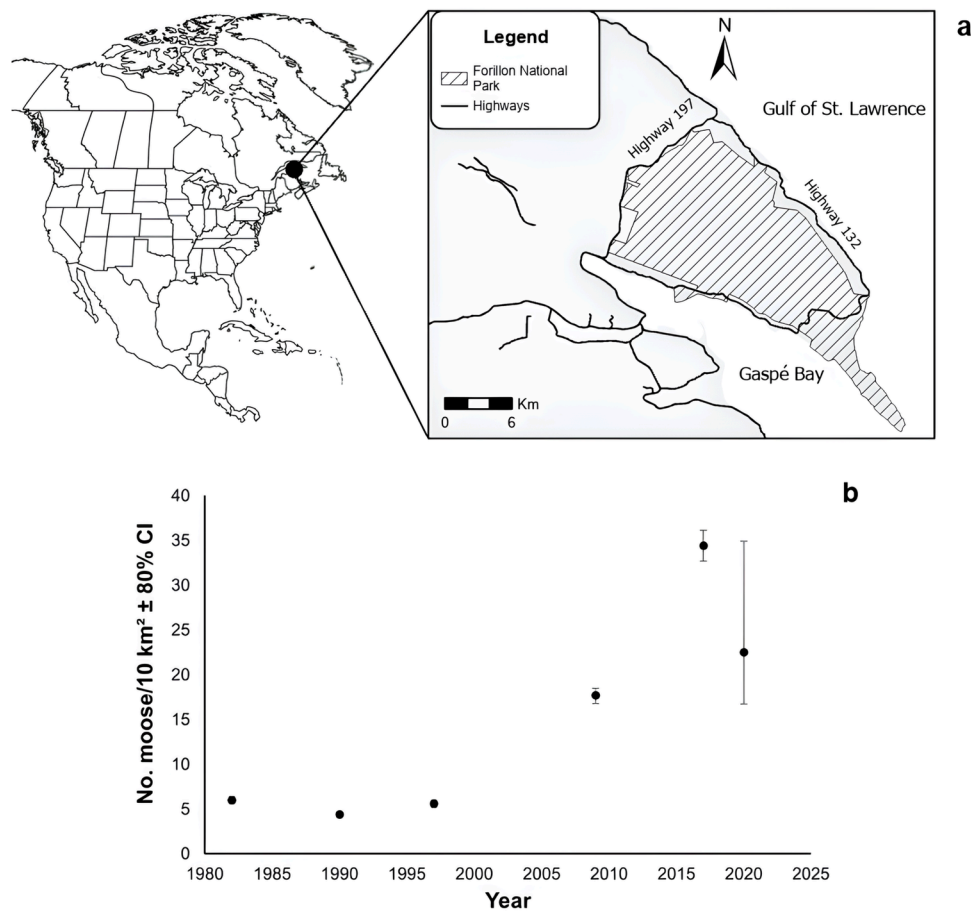


Fig. 1. (a) Location of the study area in the province of Quebec, Canada (left), and area covered by the Forillon National Park, with adjacent paved roads in thin lines (right). (b) Variation of moose density (no. of moose/10 km²) in the park between 1982 and 2020, as estimated using aerial surveys conducted in late winter.

early seral stands (Del Degan et al., 1995). A similar outbreak is under way since 2016.

Moose density in the Forillon National Park increased substantially over the last decades (Sigouin, 2018), from 0.2/km² in 1973 to 3.5/km² in 2017 (Fig. 1b). Potential incidental predators include black bears (*Ursus americanus*) and coyotes (*Canis latrans*), while the grey wolf was extirpated from the Gaspé Peninsula at the beginning of the 20th century (Georges, 1976). White-tailed deer (*Odocoileus virginianus*) is the only other large herbivore found in the area, but densities are very low (Lebel and De Bellefeuille, 2021). The winter tick (*Dermacentor albipictus*) is also present and may increase moose mortality, especially for calves (at least slightly).

2.2. Description of our population dynamics model

We used a sex- and age-structured population model to reproduce the changes observed in moose population size in the park from 1982 to 2020 (Fig. 1b), with a yearly time step. Our model is divided into different individual modules, each one simulating the effect of one of the dynamics-driving factors using the datasets described below. A flow-chart summarizing the interactions between the different modules for one time step is provided (Fig. 2), as well as a table presenting the different assumptions we made during their designing (Table 1). Analyses, model construction and simulations were all performed in R 4.2.1 (R Core Team, 2022).

Scarce data were a challenge and definitely influenced our choice of methodology. For instance, integrated population models (IPMs) are a well-suited tool for conservation ecology that can be parameterized with time series similar to ours, but they usually require additional datasets

(including capture-recapture or mark-recovery data), which were not available in our situation, to produce sensible estimates (Schaub and Abadi, 2011). Having little information about population vital rates (e.g. survival, productivity) could have been overcome by using *N*-mixture models (Royle, 2004; Madsen and Royle, 2023) to parameterize a projection matrix (Caswell, 2001), but the *N*-mixture models may not provide accurate estimates of vital rates in the presence of density dependence or environmental stochasticity (Bellier et al., 2016), which are two important features of our study area. We thus chose to rely on pattern-oriented modelling (POM), a method that we believe was better adapted to our dataset and objectives, since it allowed us to update the vital rates annually (involving, for example, harvest data, road mortality and snow depth) and build a more explicit model regarding some biological mechanisms.

The POM method relies on the principle that patterns (defined as non-random structures in the data; Grimm et al., 1996) observed at higher levels of organisation (e.g. communities, populations) hold information about lower levels (e.g. individuals), and vice versa (Grimm and Railsback, 2012; Gallagher et al., 2021). POM can be used either for model design or parameter calibration, using multiple patterns as filters to reject any model structure or set of parameter values that prevents their simultaneous emergence in the system (Grimm et al., 2005; Kramer-Schadt et al., 2007). This method is thus not fundamentally different from other rejection sampling approaches (such as Approximate Bayesian Computing, for example), except that it stresses the importance of using several patterns of various ecological scales whenever possible to improve model accuracy (Hartig et al., 2011; Grimm and Railsback, 2012). Moreover, POM is intended to provide a clear framework to make the modelling process more systematic and explicit

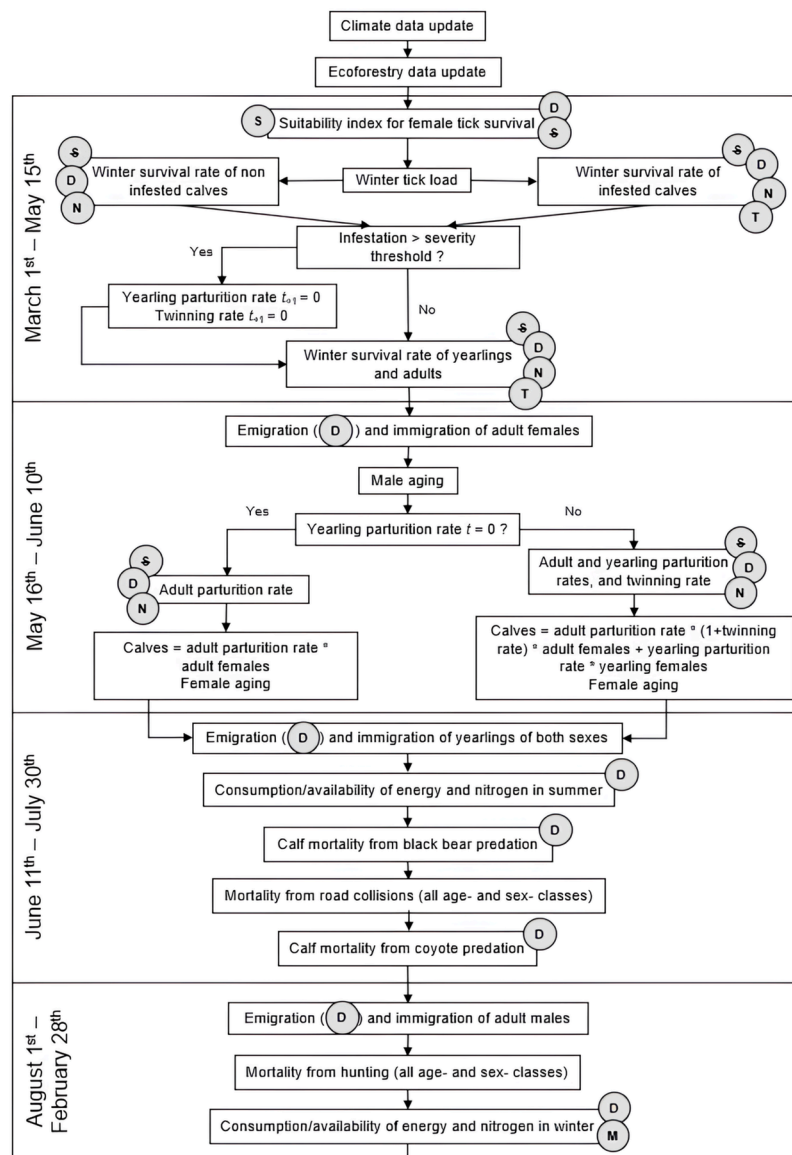


Fig. 2. Flowchart of the model for a yearly time step. The grey circles specify the influence of the population size (D: density) or some dynamics-driving factors (S: date of first snow; \$: date of snowmelt; N: NIVA index; T: winter tick load; M: mean winter snow depth).

(as researchers often go through trial and error to formulate their sub-models, but usually only disclose the final model structure; Grimm and Railsback, 2012).

The POM procedure is designed to allow researchers to obtain “structurally realistic” models and overcome data scarcity (Grimm et al., 2005; Gallagher et al., 2021). However, POM can only identify the most appropriate model structure (or parameter value) among the possibilities provided by the modeller: therefore, even the best fitting option may not be accurate if the initial choices were not relevant. In addition, the chosen patterns must match the model’s purpose, i.e. they must be discriminatory criteria for model structure or respond under the parameters to be calibrated (Gallagher et al., 2021).

Various types of information (e.g. single value, distribution) and elements (e.g. distances, genetic data, carbon stocks) can be used as patterns (Gallagher et al., 2021). We used three different patterns: the time series of abundance, sex ratio (M : F) and recruitment rate of our moose population; all of them were obtained via aerial surveys conducted between 1982 and 2020 (see Supplementary Material 1 for details about the aforementioned time series and the methods used to collect them). We divided our period of modelling into 5 subperiods

(bounded by the years in which the inventories were carried out: 1982–89, 1990–96, 1997–2008, 2009–16 and 2017–19) in order to allow the value and sensitivity (i.e. the magnitude of the effect of a change in this value on the population dynamics) of the parameters to vary over time.

The dynamics of a large herbivore population are largely dependent on its population structure, since vital rates of individuals are proven to vary with age and sex (Gaillard et al., 1998, 2000; Marescot et al., 2015). We thus decided to model our moose population as the sum of five groups of individuals: (1) calves (males and females < 1 year of age), (2) yearling (between 1 and 2 years old) females, (3) yearling males, (4) adult (> 2 years old) females and (5) adult males. The vital rates of each group are impacted to a different extent by all the dynamics-driving factors included in the model throughout a simulation (Fig. 2).

The aerial surveys did not discriminate yearlings from adults in their counts; we thus needed to approximate the number of yearlings present in the population at the beginning of each time period. Since a simulation begins on March 1st (i.e. the approximate date of the aerial surveys; Fig. 2), the number of yearlings present in the population on March 1st of year t can be calculated by multiplying the number of calves (9

Table 1
Assumptions made during model construction and parameterization.

Description	Refs.
<i>Senescence and reproduction (Section 2.2)</i>	
1. As we lacked data about the initial age structure of our population, we did not explicitly account for the effect of senescence on its dynamics.	
2. Even sex ratio at birth	Lenarz et al., 2010; Severud et al., 2019; Lee et al., 2020
3. Yearling females do not twin + maximum parturition rate of 0.5 for yearling females	Schwartz and Hundertmark, 1993; Testa, 2001; Markussen et al., 2018
4. Maximum twinning rate of 0.7 for adult females (calculated based on cows with calves)	Ruprecht et al., 2016; Boertje et al., 2019
<i>Available energy and nitrogen for moose in the habitat (Section 2.2.2)</i>	
5. A major modification of the landscape in the time interval between two forest inventories (~10 years) is unlikely in the absence of disturbance like logging or fire.	
6. Considering that the harvested population of the Seigneurie Nicolas-Riou outfitter has a quite young age structure for males (the oldest in our dataset was 5.5 years old), and that male moose usually reach their maximum body weight at 5.5–6.5 years of age, we hypothesized that the weight of males older than 5.5 in Forillon National Park would be around the same value.	Sand et al., 1995; Jensen et al., 2013
7. The mean age of adult moose (> 1 year old) in Isle Royale National Park varied from 4 to 10 years old from year to year between 1959 and 2015. However, wolf predation in this place likely influenced the age structure of this moose population, since wolves tend to select calves and individuals older than 9 years. Therefore, moose in Forillon presumably live older than in the aforementioned study area.	Hoy et al., 2020 Lake et al., 2013; Mech and Nelson, 2013
8. Digestible energy and crude protein contents in moose forage in summer $\geq$ in winter	Crête and Jordan, 1982; Crête, 1989; Rea and Gillingham, 2001; Barboza et al., 2018; Schrempf et al., 2019; Peterson et al., 2020
9. Similar body weight for male and female calves	DeBow et al., 2021
<i>Winter tick (Section 2.2.3)</i>	
10. Winter survival rate of calves infested by winter tick $\leq$ winter survival rate of non infested calves	
11. We did not account for the risk of desiccation of quiescent larvae during dry summers because our study area experiences a humid climate with much more summer rainfall compared to other studies, such as those conducted in the northeastern United States.	Addison et al., 2016; Dunfey-Ball, 2017 Jones et al., 2017, 2019; Healy et al., 2020
12. We did not consider the effect of spring temperatures on tick load as daily mean temperatures in March and April in Forillon during our study period were much lower than those linked with more severe tick-induced hair damage and loss in other study areas.	Wilton and Garner, 1993; Samuel, 2007
<i>Predation (Section 2.2.4)</i>	
13. No mortality due to predation among adult and yearling moose as these cases are rare in the literature	Ballard, 1992; Svoboda et al., 2011

months old) in the population on March 1st of year t_1 by the 9–12 months survival rate, the yearling emigration rate and the rate of yearling mortality from hunting, also accounting for some immigration, and assuming no mortality of yearlings due to predation (see Section 2.2.4). We used the number of 9-month-old calves in the population at the beginning of a given time period (March 1st of year t) as an approximation for the number of 9-month-old calves on March 1st of year t_1 . In addition, preliminary results suggested a mean 9–12 months survival rate of 0.70. Yearling emigration rate is variable, but can reach 0.30 (Ballard et al., 1991); we assumed an intermediate value of 0.15, as it is partly offset by immigration. At this early stage of our research, we hypothesized that the hunting mortality for yearlings was negligible, as our study population lives in a protected area. Thus, the number of yearlings present in the population at the beginning of each time period was set at 60 % (0.70 multiplied by 0.85, that is $1 - 0.15$) of the number of calves, respecting the sex ratio observed during the associated survey; we performed a sensitivity analysis to verify that this choice did not meaningfully impact the population trajectory.

The relations between the dynamics-driving factors and the vital rates were modeled using several equations (see Supplementary Material 2). When using non-linear convex or linear functions, the vital rates related to climate (see below) decreased too sharply, and the simulated population crashed. Thus, we used non-linear concave functions (with logarithmic-style curves), which were the most efficient to reproduce our patterns. Such a relationship between dynamics-driving factors (e.g. snow depth, winter tick engorgement) and vital rates (e.g. annual adult survival, weaning success, juvenile winter survival) was previously documented in several ungulate populations (elk: Garrott et al., 2003; Brodie et al., 2013; moose: Keech et al., 2011; DeBow et al., 2021; Alpine ibex *Capra ibex*: Mignatti et al., 2012; Sitka black-tailed deer *Odocoileus hemionus sitkensis*: Gilbert et al., 2020).

2.2.1. Climate

Climate data were downloaded from the ERA5-Land Hourly dataset on Google Earth Engine, a reanalysis obtained using satellite imagery (Munoz Sabater, 2019). We selected snow depth (cm) as our unique climate variable and averaged our hourly values to obtain daily means for our study area. Many studies reported the importance of winter severity, especially snow depth, on the dynamics of ungulates. It has been shown that during very snowy winters, moose energy expenditures associated to movement were higher and food was more difficult to find, as it is often partially buried under snow, thereby lowering moose body mass (Visscher et al., 2006; Melin et al., 2023). These cascading effects lead to reduced productivity and survival (Bishop and Rausch, 1974; Milner et al., 2013), sometimes with a time lag of 1 to 3 years (Crête and Courtois, 1997; Parker et al., 2009). The NIVA index is one of the indices frequently used to illustrate the cumulative effect of an important snow cover on wildlife over time (Potvin and Breton, 1992; Finstad, 2008; Simard et al., 2010). We used its first component to represent the relative variation in the harshness of winter conditions for moose: hereafter, NIVA will refer to the sum of daily snow depth from first snow to snowmelt (in days-cm).

Moreover, moose accumulate fat reserves during summer when the food is abundant and of high quality, and then use them to survive winter (Schwartz and Renecker, 2007; Parker et al., 2009; Shively et al., 2019). These body reserves are gradually depleted, and moose spend a long time in a negative energy balance until green-up (Schwartz and Renecker, 2007; Parker et al., 2009; Ellingwood et al., 2019). A lasting state of negative energy balance can cause weight loss, which can increase perinatal mortality (Keech et al., 2000; Milner et al., 2013) and even decrease winter and spring survival of adults (DelGiudice et al., 2011). In light of the above, we modeled the parturition rates (of yearlings and adults), the twinning rate and the late winter-early spring survival rate (later called “winter survival rate”) of calves, 1-year-olds and adults as functions of NIVA and the date of snowmelt (timing of green-up; Brown, 2011; Kautz et al., 2020; see Supplementary Material 2

for more details). We tested for a 1-year delay in the effect of NIVA on these 5 vital rates using several scenarios.

2.2.2. Available energy and nitrogen for moose in the habitat

Carrying capacity is a widely used concept in the literature, although caution is required (Chapman and Byron, 2018). It seems particularly relevant in our study area, given that the wolf's absence means that it does not exert a "top-down" control over the moose population, and because timber harvesting and moose sport hunting are prohibited in the park. Moreover, negative browsing effects of the recent high moose densities on the park's forest are now observed (Sigouin and Samson, 2022), suggesting that a shortage of food resources may have occurred in the last few years.

Metabolizable energy is among the most limiting factors for wild ungulates (Dumont et al., 2005; Parker et al., 2009; Welch et al., 2015) and is of primary importance for their performance (Illius and Gordon, 1999; Parker et al., 2009). An increasing number of studies also suggest that proteins (nitrogen) can be significantly limiting for large herbivores (Cain et al., 2017; Barboza et al., 2018; Shively et al., 2019). We therefore incorporated the concept of carrying capacity in our model by comparing the total available metabolizable energy (ME) and nitrogen (N) within the park to the total annual ME and N requirements of the moose population.

Using ArcGIS Pro 2.9 (ESRI, 2021), we used the digital ecoforestry maps of the 2nd, 3rd, 4th and 5th decennial forest inventory programs published by the Ministère des Ressources naturelles et des Forêts du Québec (MRNF) to classify forest stands in our study area as open (conifer canopy closure < 50 %) and closed habitats (conifer canopy closure > 50 %) following Crête (1989). This author evaluated the annual forage production (in kg/ha) between 0.5 and 3 m in height for the 2 types of habitat in winter (November–May) and summer (June–October) in a sector adjacent to our study area. We did not use annual updates of the ecoforestry maps, but instead had one value for each type of habitat per inventory (see Table 1 for additional details). The most precise map that we could access for the 2nd forest inventory program was composed of 16 ha tiles, compared to a finer spatial resolution of 4 ha for the 3rd, 4th and 5th inventories. We classified our forest stands the same way as for the other inventories (open and closed habitats), except that the information on the dominance of coniferous or deciduous species within mixedwood stands was not available in the digital file: we thus used the same proportion as in the 3rd inventory.

Other forest inventories conducted by park managers (in 1995, 2006 and 2015) suggested that apart from balsam fir, the mean number of twigs/ha did not change over time for the main tree species consumed by moose (see Supplementary Material 3). This may be explained by the absence of disturbance other than spruce budworm, which severely damaged only < 4 % of the park's forest (Del Degan et al., 1995). As for balsam fir, 11.1 % (11/99) of the plots surveyed in 2015 showed a very high number of twigs/ha (> 3000) while the overall median value of the 99 plots was stable between 1995 and 2015 (~400 twigs/ha). The very rich plots were located mostly within old (> 50 years old), dense stands that were partially impacted by the spruce budworm in 1983–1984, triggering the regeneration of a dense balsam fir cohort. Such a post-outbreak regeneration pattern for balsam fir has been documented in other studies conducted in Quebec (Morin, 1994; Bouchard et al., 2005; Chagnon et al., 2022). We accounted for this sharp but localized increase of food resources by making the annual forage production of balsam fir dependent on the time elapsed since the last spruce budworm outbreak. We delayed the starting point of the regeneration of balsam fir by 2–3 years (in 1986) because the triggering of the growth of a new cohort due to the canopy opening usually occurs a few (up to 5) years after the defoliation/mortality of mature trees (Blais, 1981; Bouchard et al., 2006; Virgin and MacLean, 2017). We extracted the data for the 11 concerned vegetation plots and distinguished the amount of forage produced by saplings vs. trees. We then calculated the mean production of twigs/ha for saplings in 1995, 2006 and 2015, to which we fitted an

exponential curve. We transposed this exponential growth curve to the annual forage production of balsam fir in kg/ha for 11 % of the forest while respecting the proportions.

As suggested by Crête (1989), balsam fir was not considered to be completely available when calculating the amount of resources in winter, as this species is a great source of nitrogen but is difficult to digest due to the presence of secondary metabolites such as condensed tannins (Robbins et al., 1987a; Windels and Hewitt, 2011). Instead, we hypothesized that moose would first consume all the twigs of deciduous species (Crête, 1989; Månsson, 2007; Peterson et al., 2020) and then rely on the less palatable balsam fir by the end of winter (Crête and Courtois, 1997; Desgagnés et al., 2022; Spitzer et al., 2023). Hence, we used POM to estimate the proportion of balsam fir to be added with the other variables in the calculation.

We removed the forage with a height ranging from 0.5 m to the mean value of daily snow depth for the winter period (Hanley et al., 2012). Moreover, we excluded the part of the forage that moose calves cannot reach, as they are smaller than adults, making the forage between 1.5 m and 3 m in height available only for yearlings and adults. We modeled the requirements of calves so that they rely on forage 14 weeks out of 20 in summer, because although they suckle until late August, they already feed mainly on forage by mid-July (Gasaway and Coady, 1974; Schwartz, 2007).

We used data collected on 70 moose harvested by sport hunters at the Seigneurie Nicolas-Riou outfitter (Quebec; 48°14'00" N, 68°45'00" O; 320 km away from Forillon National Park) to build equations relating moose age (for males and females separately) to body weight. As done elsewhere (Wallin et al., 1996), we fitted a non-linear model to the weight data for both sexes (males: $n = 33$, $R^2 = 0.85$, P -value < 0.001; females: $n = 37$, $R^2 = 0.88$, P -value < 0.001). We converted field-dressed weights into whole weights using the regression equation calculated by Jensen et al. (2013) ($n = 154$; $R^2 = 0.93$). Having no information regarding the age structure of our population in Forillon, we estimated the mean age of adult males and females via POM (setting a range of 5 to 12 years old for both sexes; see Table 1 for additional details).

The values used to approximate the total available ME (kcal) and N (g) within the study area and the total ME and N requirements of the population for both winter and summer of each year considered in our model are listed in Table 2. We performed a sensitivity analysis on these values, i.e. we increased and decreased each one by 5 % while keeping the others constant, to verify that a slight modification did not meaningfully impact the results of the model simulations. The most sensitive values were estimated via POM. We chose ME and N requirements that allow body maintenance, gestation and lactation, antler growth, calf growth and a 30 % body mass gain in summer (Schwartz et al., 1988; Reese and Robbins, 1994; Moen and Pastor, 1998).

The energetic balance (see Section 2.2.1) can become negative in winter when moose density is high because individuals deplete the available winter forage more quickly (Boertje et al., 2007; Paragi et al., 2015). We incorporated an effect of density on the different vital rates, respecting the sequence described by Eberhardt (1977, 2002) and Gaillard et al. (1998): the survival rate of calves is the first to be impacted when density increases, followed by the age at first reproduction, parturition rate of adult females and then survival rates of adults. Consequently, when the ratio between the total population requirements in the limiting nutrient and its availability in the habitat exceeded a given threshold in winter, the survival rate of calves (infected or not by winter tick) decreased. We set this first threshold at 0.5, as was done elsewhere (Rempel et al., 2021). Similarly, when this ratio reached a second threshold (between 0.5 and 0.8, estimated with POM), the parturition rate of yearling females was set to 0 and the twinning rate was reduced (decrease estimated via POM, with a maximum of 0.25 as did Rempel et al., 2021). When the ratio of population requirements/availability of the limiting nutrient exceeded a third threshold value (between the second threshold and 0.9, estimated with POM), the parturition rate of adult females was reduced (decrease

Table 2

Values used to calculate the total available metabolizable energy (kcal) and nitrogen (g) and the total metabolizable energy and nitrogen requirements of the population within the study area in winter and in summer for each year covered by the model.

Description	Value ¹	Unit	Refs.
<i>Availability</i>			
Annual production of leaves between 0.5 and 3 m in height in open habitat (summer forage) ²	167	kg-dry weight ³ /ha	Crête, 1989
Annual production of leaves between 0.5 and 3 m in height in closed habitat (summer forage) ²	44	kg-dry weight/ha	Crête, 1989
Annual production of deciduous twigs between 0.5 and 3 m in height in open habitat (winter forage) ²	28	kg-dry weight/ha	Crête, 1989
Annual production of deciduous twigs between 0.5 and 3 m in height in closed habitat (winter forage) ²	8	kg-dry weight/ha	Crête, 1989
Annual production of balsam fir twigs between 0.5 and 3 m in height in open habitat ²	387	kg-dry weight/ha	Crête, 1989
Annual production of balsam fir twigs between 0.5 and 3 m in height in closed habitat ²	185	kg-dry weight/ha	Crête, 1989
Mean digestible energy content of summer forage	POM	kcal/g-dry weight	Rea and Gillingham, 2001; Barboza et al., 2018; Schrempp et al., 2019; Peterson et al., 2020
Mean digestible energy content of winter forage	POM	kcal/g-dry weight	
Digestible energy content of balsam fir	POM	kcal/g-dry weight	
Efficiency of energy metabolism	78	%	Robbins, 1993
Mean crude protein content of summer forage ⁴	POM	g/100 g-dry weight	Crête and Jordan, 1982; Crête, 1989; Rea and Gillingham, 2001; Schrempp et al., 2019; Peterson et al., 2020
Mean crude protein content of winter forage ⁴	POM	g/100 g-dry weight	
Crude protein content of balsam fir in summer ⁴	POM	g/100 g-dry weight	
Crude protein content of balsam fir in winter ⁴	POM	g/100 g-dry weight	
Efficiency of protein metabolism	82	%	Robbins, 1993
Kjeldahl nitrogen conversion factor	6.25	-	
<i>Requirements</i>			
Required intake of metabolizable energy in summer ⁵	345	kcal/kg body weight ^{0.75} /day	Moen and Pastor, 1998
Required intake of metabolizable energy for yearlings and adults in winter (body maintenance)	144	kcal/kg body weight ^{0.75} /day	Schwartz et al., 1988; Pekins, 2020
Required intake of metabolizable energy for calves in winter (growth)	181	kcal/kg body weight ^{0.75} /day	Tarr and Pekins, 2002; Pekins, 2020
Additional requirement of metabolizable energy for gestation in winter ⁶	101.6 83.6	kcal/ singleton/day kcal/twin/ day	Robbins and Moen, 1975
Required intake of N for body maintenance ⁷	0.254	g/kg body weight ^{0.75} /day	Schwartz et al., 1987; Schwartz and Renecker, 2007

Table 2 (continued)

Description	Value ¹	Unit	Refs.
Required intake of N for protein deposition (30 % mass gain in summer)	17.3 13.0	g/male/day g/female/day	Moen and Pastor, 1998
Required intake of N for gestation ⁶	508	g/singleton	Robbins and Moen, 1975
Required intake of N for lactation ⁸	418 3800 3173	g/twin g/singleton g/twin	Reese and Robbins, 1994; Schwartz and Renecker, 2007
Required intake of N for antler growth ⁹	780 120	g/adult male g/yearling male	Moen and Pastor, 1998

¹ The values noted as 'POM' were estimated with pattern-oriented modelling.

² Habitats with conifer canopy closure < 50 % are open; habitats with conifer canopy closure > 50 % are closed.

³ The mass values were standardized by removing the water content and expressed in kg or g of dry weight (dry-weight).

⁴ Converted in digestible protein using the equation of Robbins et al. (1987b).

⁵ Calculated to meet a 30 % gain in body mass throughout the summer, and energy requirements for late gestation, lactation and antler growth.

⁶ Calculated with a mean birth mass of 17 kg for singletons and 14 kg for twins (Schwartz and Hundertmark, 1993; DelGiudice and Severud, 2016; McDonough et al., 2022).

⁷ This value was tripled for weaned calves because of their rapid growth rate (Ullrey et al., 1967; Schwartz and Renecker, 2007).

⁸ Calculated for 120 days of suckling (using Figs. 1 and 2 in Reese and Robbins, 1994).

⁹ Calculated for a mean of 13 kg antlers for adult males and 2 kg antlers for yearling males (Bubenik, 2007).

estimated in the same way as for the twinning rate). Finally, when the ratio exceeded a fourth threshold value (between the third threshold and 1, estimated with POM), the yearling and adult survival rates decreased (maximum decrease of 0.2: Rempel et al., 2021).

2.2.3. Winter tick

The moose is the main host of the winter tick, which seems to become more and more abundant with the changing climate and frequently causes widespread mortality of calves in North America since 2000 (Samuel, 2004; Jones et al., 2017, 2019). The Gaspé Peninsula is no exception, despite its relatively cold climate less suitable to tick development, as 96 % of the moose sampled south of the St. Lawrence River in autumn 2012–2014 were hosting ticks (Ministère des Forêts, de la Faune et des Parcs, 2016). The lifecycle of winter ticks has five stages: (1) drop-off of adult females from host in March–April, (2) egg laying and hatching before June, (3) larvae quiescence in the ground litter during summer, (4) questing from mid-September to the offset of winter, and (5) growth on the host (Samuel, 2004). We did not have accurate data to estimate annual tick load of moose (i.e. the number of winter ticks per individual), so we relied on a literature review and decided to focus on two key periods of the tick's lifecycle that are largely influenced by climate: drop-off and questing.

Whether or not the ground is still covered by snow when adult tick females drop from their host is significant because they may die before laying eggs (Drew and Samuel, 1986). We thus computed the date of snowmelt for each year and built a suitability index for female tick survival. We did the same for the date of first snow, since it terminates the questing period (Samuel, 2004); if this date was posterior to the date of first prolonged cold (the last of 3 consecutive days with mean temperature < 0°C), which reduces the activity of questing larvae, the latter was computed instead (Samuel, 2007; Holmes et al., 2018). We also considered moose density as a factor influencing tick load because the more hosts available, the more parasites survive and reproduce (Samuel, 2004, 2007; Dunfey-Ball, 2017). In order to test whether one of these 3 factors (date of snowmelt, date of first snow/cold or host density) had a prominent effect on the final tick load, we added multipliers (estimated via POM) to each of them to allow a variation in their respective weight

in the calculation of the suitability index for female tick survival between the simulations.

The prevalence (i.e. the percentage of moose infested by winter ticks) was estimated with the POM method. Pouchet (2023) found that $40 \pm 30\%$ of the moose in Gaspésie were hosting ticks. We thus tested a range of 10 to 70 % (i.e. $40 \pm 30\%$ following Pouchet, 2023) of prevalence with POM. However, the results of this recent study may not be representative of the reality in the '80s, so we reduced the lower bound from 10 % to 0 % for all our time periods except the most recent (2017–2019).

For a given year t in the model, the tick load faced by moose in spring is determined based on the three criteria cited above. The possible mean tick load in our model ranged from 0 to 45,000 ticks per moose, which corresponds to values observed in the wild (Musante et al., 2007; Jones et al., 2019). However, the type of equation linking the annual tick load to our female tick survival index was uncertain. We tested three types of equation: linear, logarithmic or exponential, with parameters estimated with POM. The linear and logarithmic equations led to mean tick loads (i.e. no. of ticks/moose) ranging from 0 to 18,000, and from 0 to 35,000, respectively, for the 1990–1996 period. The same trend was observed for the 1997–2008 period, with respective ranges of 0–30,000 and 0–37,000. In comparison, tick load on calf hides collected between 2014 and 2016 in New Hampshire (where climate is much more favorable to winter tick survival and reproduction) ranged from 19,000 to 95,000, with a mean of 47,000 (Jones et al., 2019). From 1977 to 1991, Samuel (2004, 2007) documented a mean tick load $< 10,000$ ticks/moose when moose density was under 1 moose/km² in Elk Island National Park (Alberta), which is almost at the same latitude as Forillon National Park. Furthermore, using the linear or logarithmic equation would have led to mean tick loads $> 35,000$ for multiple years between 2009 and 2016 for a non-negligible proportion of simulations, which would have greatly reduced winter calf survival, and hampered adult reproduction and survival. This is obviously not the case considering the rapid increase in moose abundance, which roughly doubled during this time period. Preliminary results rather suggested that successful simulations for 2009–2016 were consistently associated with relatively low mean tick loads ($< 20,000$). A recent study also showed that both winter tick load and winter tick prevalence in our study area are among the lowest in Quebec (Pouchet, 2023). Thus, we selected the exponential-type equation as the best fitting in our situation, and we did not test the two other forms for the three remaining time periods.

Tick bites can impair moose health in three main ways: first, tick-induced self-grooming lowers the appetite and the time allocated to feeding and thus decreases energy reserves (Samuel, 2004). Second, hair damage and loss due to grooming result in a higher energy cost for maintaining body temperature (Samuel, 2004). Finally, moose can experience anemia due to blood loss from ticks and must spend supplementary energy to replace it (Samuel, 2004; Musante et al., 2007). All these processes can trigger or worsen a state of negative energy balance in winter (Ellingwood et al., 2019; Rosenblatt et al., 2021), which can affect moose survival rate. Since grooming, hair damage and blood loss are proportional to tick load (Mooring and Samuel, 1998; Samuel, 2004), we calculated the winter survival rate of infested calves based on tick load, NIVA and the date of snowmelt (see above). We assumed adult and yearling moose are unlikely to die from the effects of ticks due to higher body weight and blood volume (Samuel, 2007; Musante et al., 2007; Jones et al., 2019), except in circumstances of high tick load during several consecutive years (DeBow et al., 2021; Harris et al., 2021). A year t was marked as “year of severe infestation” if the tick load was higher than 35,000 ticks per individual (Healy et al., 2020). In such cases, the parturition rate of yearling females and the twinning rate were automatically set to 0 for the year $t+1$ (in accordance with results obtained by Musante et al., 2007, 2010; Jones et al., 2017, 2019). Moreover, we implemented a function that added mortality for yearlings and adults if this tick load threshold was exceeded for two successive years or more (estimated with the POM method, with a maximum mortality rate of 0.15 as it was seen in DeBow et al., 2021).

2.2.4. Predation

Black bears and coyotes are the only potential predators of moose in the Forillon National Park. It has been shown that black bears are a threat to moose calves, mainly during their 4 to 6 first weeks of life (Zager and Beecham, 2006; Ballard and Van Ballenberghe, 2007). Black bear density in the park was probably under 2.0 bears/10 km² during the '80s (Ministère de l'Environnement, de la Lutte contre les Changements climatiques, de la Faune et des Parcs du Québec [MELCCFP], unpublished data). It was then estimated to range between 2.3 and 4.7 bears/10 km² by the end of the 1990s (Leblanc and Huot, 2000), an estimation confirmed in 2015 (Pettigrew et al., 2021). The results of the most recent survey (2020) suggest that the bear density is now between 4 and 7 bears/10 km² (Gaudet-Boulay and Sigouin, unpublished data). In our model, we thus made the bear density vary between 1.0 and 2.0 bears/10 km² from 1982 to 1990 using a normal distribution (mean = 1.5, SD = 0.2), between 2.3 and 4.7 bears/10 km² from 1991 to 2017 (mean = 3.5, SD = 0.55) and between 4.0 and 7.0 bears/10 km² from 2018 to 2020 (mean = 5.4, SD = 0.6). The length of the period when calves are vulnerable to black bear predation (between 30 and 90 days according to authors: Ballard et al., 1980; Zager and Beecham, 2006; Ballard and Van Ballenberghe, 2007) was estimated via POM. Similarly, the proportion of adult bears (> 2 years old) in the population (between 0.60 and 0.85: Hellgren and Vaughan, 1989; Bales et al., 2005; Hébert et al., 2009), the age class that can predate moose, was estimated with POM. Indeed, a sensitivity analysis showed that the response of the simulated patterns to a change in the values of these two parameters was not negligible. The kill rate of bears on moose calves was also estimated via POM, and we made it vary annually in proportion to the ratio between moose density and bear density (i.e. moose/bear density ratio) because the higher the moose numbers with respect to bears, the higher the probability of encounter.

Coyotes, on the other hand, usually kill moose calves that are up to 6 months old (Wolfe, 1974; Crête and Desrosiers, 1995; but see Benson and Patterson, 2013). The coyote colonized the Gaspé Peninsula during the '70s (Georges, 1976), and its density was estimated between 0.7 and 0.8 coyotes/10 km² in the park before 2000 (Fortin, 1995), but recent harvest data suggest that it has increased since then (Données Québec, 2025a). However, the populations of white-tailed deer, the main prey of the coyote, have been collapsing since 2015 in Gaspésie (Données Québec, 2025b). We thus hypothesized that the coyote density in our study area declined slightly in response to this collapse (P. Etcheverry and D. Sigouin, pers. comm.). As we did for black bears, we used normal distributions to make the coyote population in the park vary in size, ranging from 0.7 to 0.8 coyotes/10 km² for the 1982–2000 period (mean = 0.75, SD = 0.02), from 0.8 to 1.0 coyotes/10 km² for 2001–2015 (mean = 0.90, SD = 0.06) and from 0.7 to 0.8 coyotes/10 km² for 2016–2020 (mean = 0.75, SD = 0.02). The kill rate of coyotes on moose calves was estimated using POM but was allowed to vary annually in proportion to the moose/coyote density ratio.

As we parameterized our model, we noted that the values of kill rates that we found in the literature very frequently yielded high predation rates on calves for both bears and coyotes, which reduced the ability of our model to reproduce the patterns observed in the field. Thus, we implemented maximum values for predation rates in the model to allow lower values of predation rates to be explored as well, by forcing the model to select from a lower range of values. For each time period, we tested several values for this maximum, with 5 % intervals (e.g. for 1997–2008, we tested maximum predation rates of calves of 25 %, 30 %, 35 % and 40 %). For each time period, we stopped testing higher or lower values when the percentage of simulations reproducing our patterns markedly decreased, or the deviation between simulated and observed patterns markedly increased (see below). For a given maximum predation rate, the model was free to explore all the values below this limit, including all the possible decimals.

2.2.5. Dispersal

Although moose movement across the park boundaries might be constrained by the peninsular situation of the park and the presence of Highway 197 (and its urban development), emigration and immigration are still possible. Indeed, moose are regularly seen crossing Highway 197 in both directions, and this is confirmed by the movements of 21 GPS-collared females, tracked since 2020 (P. Etcheverry, *unpublished data*). We thus allowed individuals from all our groups (excluding calves) to enter or leave the park once a year in proportions estimated using POM, with a higher probability of dispersal for yearling individuals (Ballard et al., 1991; Labonté et al., 1998; Dodge et al., 2004). We tested two alternative hypotheses for this emigration process: (1) in the case of a positive density dependence (PDD), emigration would be low but greater than zero at low densities (relative to carrying capacity), essentially because competition for food resources would be weak and leaving the natal range would offer only a subtle advantage, and would thereafter increase at higher densities due to a more intense competition for both food resources or mates (literature review by Hundertmark, 2007; Rempel et al., 2021); (2) according to a negative density dependence (NDD) scenario, the emigration rate would decrease at high densities because of aggressive behaviour in older males, a low gain from dispersal since all areas are occupied or because of a poor body condition that hinders travel (Hjeljord, 2001).

Regarding immigration rates, we hypothesized that they would display no particular pattern and vary randomly between years, as the outsiders do not know the environmental characteristics (e.g. density, habitat quality, etc.) in the park before entering it (Akçakaya et al., 1999). Therefore, we used normal distributions with means and standard deviations estimated using the POM method.

2.2.6. Hunting and road accidents

The number of moose harvested by sport hunters is normally known with precision, as reporting big game harvest is a legal requirement in the province of Quebec. Annual harvesting data were taken from the Wildlife Incident Management System of the park for the period 1982–2019. We accounted for all mortalities that occurred within 5 km of the park (Chamberland and Sigouin, 2017). We also subtracted from the population the individuals that were killed by vehicle collision on Highways 132 and 197 (see Supplementary Material 4). For hunting and

safe, we chose to generate respectively 120, 140 and 160 replicates for each simulation. Unfortunately, the mean for the moose abundance pattern could not be perfectly stabilized for the last three time periods and kept varying (< 8 individuals) between replicates, even when we increased the number of replicates to over 300. This did not impact the results, as they were calculated over all the “successful” simulations (see below).

We had a total of 83 parameters to estimate with the POM strategy (see Supplementary Material 2, which presents a comprehensive list of these parameters with their respective ranges, all determined based on careful literature reviews, along with the associated equations in the different modules). However, according to Grimm and Railsback (2012), the models calibrated using the POM method usually include 10 to 20 parameters to be estimated. These should be restricted to the ones for which the value is particularly uncertain or to which the model is very sensitive. Besides, as far as we know, no published study used POM to estimate more than 17 parameter values (Topping et al., 2012). We thus managed to reduce the number of variables from 83 to 20 following the process described below (see Fig. 3 for a visual support). The results without fixed parameter values are available in Supplementary Material 5 for comparison.

We ran 100,000 simulations sampling a different value for each parameter to calibrate by POM for each subperiod and each scenario of our population model to cover a large part of the possible combinations for the parameter values (see Table 3 for a summary of the tested scenarios). At the beginning of each simulation, parameter values were independently sampled from uniform distributions (this only concerns the parameters estimated with POM). A simulation was selected if the 95 % confidence intervals (CI) around the simulated values (means of the replicates) were included in the 80 % CI around the observed values (aerial surveys) for the three patterns simultaneously. For each scenario, we calculated the success rate as the percentage of tested parameter sets that were retained. We plotted these values and searched for a clear breakpoint between the “high” and “low” success rates. We selected the scenarios for which the success rates were above this break (step B in Fig. 3).

For each tested parameter set, the deviation between simulated and observed values was calculated as follows:

$$\text{Deviation} = |obs_{POP} - sim_{POP}|/80CI_{POP} + |obs_{sex_ratio} - sim_{sex_ratio}|/80CI_{sex_ratio} + |obs_{recruitment} - sim_{recruitment}|/80CI_{recruitment} \quad (\text{Eq. (1)})$$

road mortalities, our datasets did not differentiate adult individuals (> 2 years old) from yearlings. Since they are separated in our model, we removed individuals from each category in proportion to their presence in the population (e.g. if in year t a total of 7 males > 1 year old died from hunting, and yearling males accounted for $1/7$ of the male segment of the population, then 1 yearling male and 6 adult males died).

2.3. Model parameterization

In order to account for stochasticity in the model, we chose to do multiple replicates for each tested parameter set (Rangel et al., 2007; Desforges et al., 2021). This allowed us to avoid selecting a set of parameter values that “accidentally” reproduces the observed patterns as a result of stochasticity. For a given parameter set, we did several tests, increasing the number of replicates until the mean values for our three patterns stopped varying. A total of 100 replicates was the minimum required to stabilize the means of sex ratio and recruitment rate for the periods 1982–1989 and 1990–1996. This number increased to 120 replicates for the periods 1997–2008 and 2017–2019, and 140 replicates for 2009–2016 due to more stochasticity. Based on the above, and to be

where obs_{POP} , obs_{sex_ratio} and $obs_{recruitment}$ are respectively the moose abundance, sex ratio and recruitment rate derived from the aerial surveys; sim_{POP} , sim_{sex_ratio} and $sim_{recruitment}$ are the same values obtained from the model (means of the replicates), and $80CI_{POP}$, $80CI_{sex_ratio}$ and $80CI_{recruitment}$ are respectively the 80 % confidence intervals around obs_{POP} , obs_{sex_ratio} and $obs_{recruitment}$. The deviation ranged from 0 to 3.

For each selected scenario, we ran the number of simulations required to obtain at least 5000 successful parameter sets, which was necessary to have stable means for all the parameters. We selected the parameter set for which the deviation between simulated and observed values was smallest (step D in Fig. 3). We then performed sensitivity analyses: for each selected scenario and each period of time, we fixed all the parameter values to those of the parameter set with the least deviation and tested the sensitivity of the results (the simulated values of our three patterns) to variations in these values. We did that by increasing and decreasing by 5 % every value estimated via POM one at a time (as seen in Smythe et al., 2019; Desforges et al., 2021). Please note that, for instance, a 5 % increase of the value of one of the parameters involved in the calculation of the adult female parturition rate does not necessarily translate in a 5 % increase of the adult female parturition rate itself.

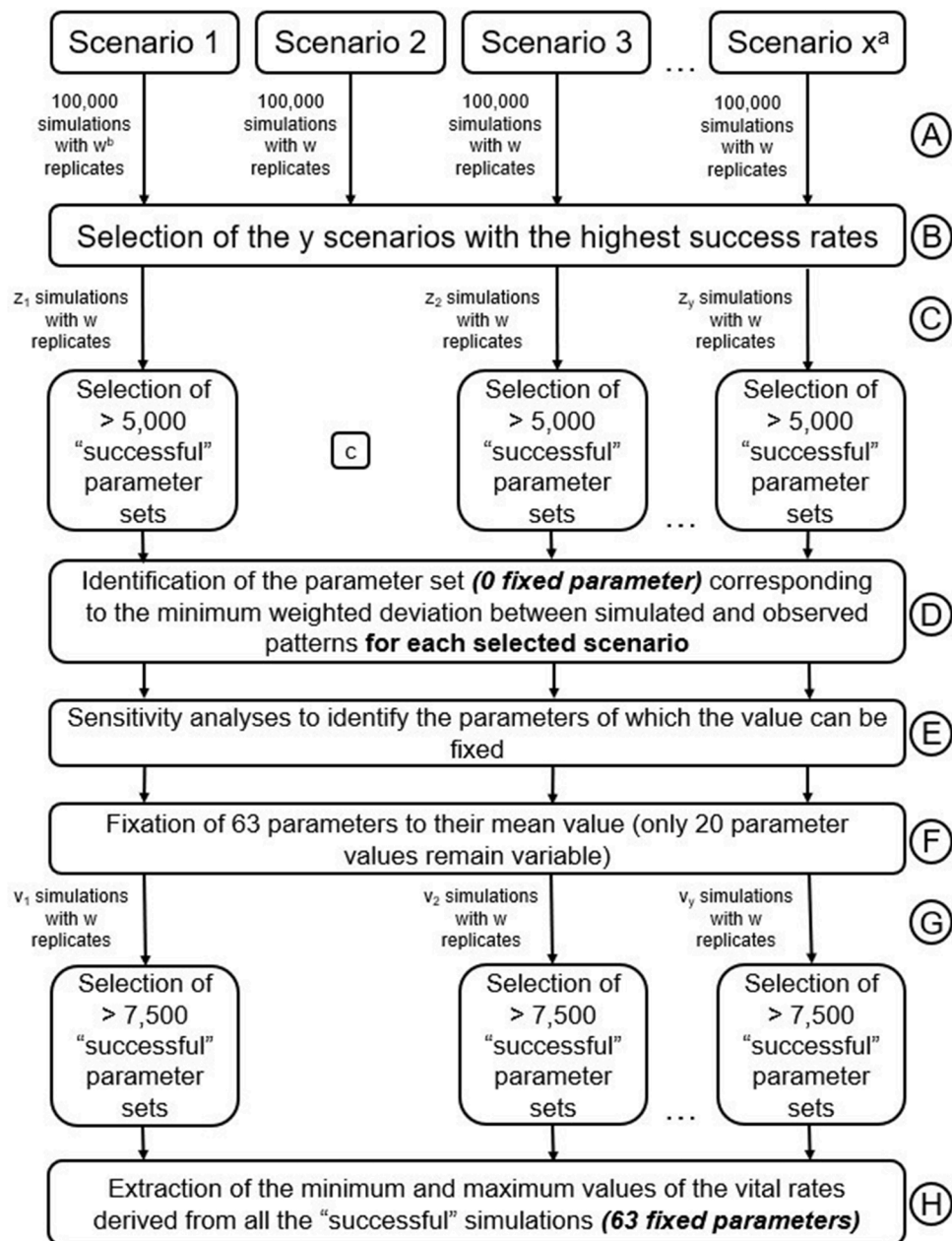


Fig. 3. Summary of the steps involved in the parameterization of the model. This sequence is conducted for each of our five time periods. z and v represent different numbers of simulations. ^a $x=8$ for 1982–1989 and 1990–1996, and $x=16$ for 1997–2008, 2009–2016, and 2017–2019. ^b $w=120$ for 1982–1989 and 1990–1996, $w=140$ for 1997–2008 and 2017–2019, and $w=160$ for 2009–2016. ^c The “missing box” under scenario 2 illustrates that this scenario was not selected (i.e. it had a low success rate compared to the others) and thus did not undergo the next steps of parameterization.

Following Grimm and Railsback (2012), the results of these sensitivity analyses (available in Supplementary Material 6) were used to define which of our 83 parameters could be fixed for each period of time. When making this choice, we made a trade-off between the sensitivity and several other criteria, namely the necessity to leave at least one unfixed parameter value in each module to allow flexibility and the possible shift of the mean value of a parameter with respect to the mean of its range (another way to measure its sensitivity if not detected by the sensitivity analysis).

Once we knew which parameters could be fixed, we calculated their mean values with all the successful parameter sets (step F in Fig. 3). We rounded them to three significant digits, which was the highest level of precision that we could obtain (even using 25,000 parameter sets did not improve precision). We consider this level of precision suitable in regard of the amplitude of the parameter ranges. Indeed, the last significant

digit was always well below the $\pm 5\%$ tested in the sensitivity analysis. Moreover, most of the fixed parameters had a mean value really close, if not equal, to the mean of their range, indicating that the model could manage to reproduce the patterns whatever the values of these parameters. A summary of the fixed parameters and their values for each subperiod of time is presented in Supplementary Material 7.

For the 20 remaining parameters, we performed a second step of POM, running as many simulations as needed to obtain a substantial number of “successful” parameter sets for each time period and each selected scenario (step G in Fig. 3). In order to stay close to the guidelines of use of POM and avoid overfitting (Gallagher et al., 2021), the results presented in Table 4 were calculated over all the “successful” simulations from all the selected scenarios for each time period, instead of only focusing on the parameter set leading to the smallest deviation. No transformed scale was applied to our simulated vital rates.

Table 3

Summary of the tested scenarios for each period of time. Blank cells represent scenarios that were tested but not selected, while shaded cells represent the selected scenarios. For the first two periods, the two dispersal scenarios were merged into one: indeed, moose density remained relatively low and stable between 1982 and 1996, so the two patterns of emigration yielded similar figures.

Scenario of delay of winter effects on the vital rates	Time period							
	1982–89	1990–96	1997–2008		2009–16		2017–19	
	Dispersal scenario							
	-	-	PDD ¹	NDD ²	PDD	NDD	PDD	NDD
1. No delay for all								
2. Delay: reproduction								
3. Delay: yearling and adult survival								
4. Delay: yearling and adult survival, and reproduction								
5. Delay: calf survival								
6. Delay: calf survival, and reproduction								
7. Delay: calf survival, and yearling and adult survival								
8. Delay for all								

¹PDD = positive density dependence in dispersal.

²NDD = negative density dependence in dispersal.

3. Results

We ran several million simulations using pattern-oriented modelling to reproduce the variations in moose abundance, sex ratio and recruitment rate for 5 periods of time between 1982 and 2020. Between 2 and 5 scenarios were selected for each time period (Table 3). The percentage of simulations of the selected scenarios that successfully reproduced the observed patterns of moose density, sex ratio and recruitment rate (hereafter “success rate”) varied between 4.2 and 9.0 % for 1982–1989, 14.0 and 15.0 % for 1990–1996, 2.1 and 2.9 % for 1997–2008, 1.5 and 3.3 % for 2009–2016, and 30.6 and 32.9 % for 2017–2019. The sensitivity analysis revealed that the most sensitive parameters of the model were those coding for the winter survival rate of non-infested calves, adult male and female survival rates and adult female parturition rate for all time periods (Supplementary Material 6). Overall, variations in the values of the parameters linked with calf survival rate had the highest impact on moose abundance. Changes in the parameters linked with adult survival rates had the greatest effect on sex ratio, and variations in the parameters coding for adult female parturition rate mostly impacted recruitment rate.

3.1. The impact of moose density on population dynamics

The ranges of values of winter calf survival rate derived from the selected simulations were large and variable from one time period to another (although overlapping), and affected by density (Table 4). Overall, winter survival rates of yearlings and adults were stable between 1982 and 1996, but slowly decreased from 1997 to 2019 (Table 4). The reproductive rates were mostly stable between 1982 and 2008 (Table 4). The parturition rate of yearling and adult females, along with the twinning rate, markedly decreased as moose density increased. Indeed, the moose abundance became progressively closer to the carrying capacity of the park over time, and then strayed from it during the last time period. According to the selected simulations for the 2009–2016 period, the moose carrying capacity was estimated to be between 2.3 and 4.5/km² (Table 4), and may have been exceeded for several years between 2014 and 2020. The ratio of moose nutritional requirements/availability in summer stayed under 0.30 during all the

time periods. When comparing the requirements/availability ratios for energy (ME) and nitrogen (N), energy was the less abundant nutritional resource in summer, as the ratio was about twice as high as for nitrogen. However, no clear pattern was observed for winter, as nitrogen was more limiting in some simulations while energy was more limiting in others. The differences (calculated by subtracting the requirements/availability ratio of energy from that of protein) were slight from 1982 to 1996 (ranging from -0.03 to 0.04) and intensified afterwards (ranges of -0.08–0.29 in 1997–2008, -0.23–0.39 in 2009–2016, and -0.18–0.23 in 2017–2019).

3.2. Predation, winter weather and parasitism influence moose abundance

Overall, our model suggests that the proportion of calves killed annually by black bears and coyotes decreased between 1982 and 2008, and remained approximately stable afterwards (Table 4). The calf survival rate also appeared to be sensitive to winter severity and length (variations detailed in Supplementary Material 8). The most successful scenarios for the periods 1982–1989, 1990–1996 and 2009–2016 all included a 1-year delay in the effects of cumulative snow depth (NIVA) and date of snowmelt on the reproductive performance of females (Table 3). On the contrary, for the periods 1997–2008 and 2017–2019, the scenarios with no delay in the effects of winter on reproductive rates were more successful. The ranges of values of winter survival rate of calves infested by the winter tick almost completely overlapped those of non-infested calves, except for the 2017–2019 period (Table 4). The winter tick prevalence was highly variable between simulations (Table 4). Winter tick load increased with time, but never exceeded the threshold of severe infestation (35,000 ticks/moose). Winter tick did not affect the survival rates of yearlings and adults or the reproductive rates (Table 4).

3.3. Hunting mortality and dispersal are sex-biased

Hunting mortality increased with time for all sex and age classes (Table 4). The survival rates during autumn (i.e. hunting season) were lower and decreased more for males than for females and calves. The

Table 4

Ranges of values (min–max) of the vital rates and some environmental parameters from all the selected simulations for each subperiod. For each vital rate in the “winter/spring survival” and “reproduction” sections, the first line indicates the “gross value”; the line “*after winter tick*” indicates the value of the vital rate after considering the effect of winter tick; and the line “*after density dependence*” indicates the “final value” after taking into account the effect of winter tick as well as the effect of moose density. A “-” indicates that the value is identical to that of the line above.

	Time period				
	1982–1989	1990–1996	1997–2008	2009–2016	2017–2019
Survival					
<i>Winter/spring (end of hunting season–May 31st)</i>					
Calves not infested by winter tick	0.64–0.85	0.46–0.91	0.60–0.93	0.61–0.87	0.56–0.85
<i>after density dependence</i>	-	-	0.54–0.87	0.54–0.82	0.46–0.76
Calves infested by winter tick	0.00–1.00	0.00–1.00	0.51–1.00	0.00–1.00	0.53–0.79
<i>after density dependence</i>	-	-	0.39–1.00	0.00–1.00	0.42–0.67
Yearling females	0.94–0.99	0.94–1.00	0.94–0.96	0.94–0.96	0.91–0.94
<i>after winter tick</i>	-	-	-	-	-
<i>after density dependence</i>	-	-	0.89–0.96	0.87–0.96	0.83–0.94
Yearling males	0.94–0.98	0.94–1.00	0.95–0.97	0.94–0.96	0.90–0.95
<i>after winter tick</i>	-	-	-	-	-
<i>after density dependence</i>	-	-	0.90–0.97	0.86–0.96	0.83–0.95
Adult females	0.92–0.97	0.91–0.98	0.93–0.99	0.93–0.99	0.90–0.98
<i>after winter tick</i>	-	-	-	-	-
<i>after density dependence</i>	-	-	0.91–0.98	0.92–0.98	0.80–0.98
Adult males	0.92–0.99	0.91–0.98	0.92–0.98	0.92–0.99	0.90–0.98
<i>after winter tick</i>	-	-	-	-	-
<i>after density dependence</i>	-	-	0.86–0.98	0.84–0.98	0.82–0.98
<i>Summer (June 1st–start of hunting season)</i>					
Proportion of calves killed by predators	0.52–0.66	0.32–0.56	0.24–0.40	0.18–0.40	0.20–0.45
Combined kill rate (calves/predator/year)	0.54–0.85	0.23–0.55	0.32–0.79	0.41–1.34	0.29–1.35
Total summer survival of calves (<i>predation + vehicle collisions</i>)	0.32–0.46	0.44–0.67	0.59–0.75	0.59–0.81	0.54–0.80
Yearling females (<i>vehicle collisions</i>) ¹	1.00–1.00	1.00–1.00	0.99–0.99	0.99–1.00	0.99–1.00
Yearling males (<i>vehicle collisions</i>) ¹	1.00–1.00	1.00–1.00	1.00–1.00	1.00–1.00	1.00–1.00
Adult females (<i>vehicle collisions</i>) ¹	1.00–1.00	0.99–0.99	0.98–0.99	0.99–0.99	0.99–0.99
Adult males (<i>vehicle collisions</i>) ¹	1.00–1.00	1.00–1.00	0.99–1.00	0.99–1.00	1.00–1.00
<i>Autumn (hunting season)</i>					
Calves ¹	0.98–0.99	0.97–0.99	0.97–0.98	0.94–0.96	0.93–0.97
Yearling females ¹	1.00–1.00	1.00–1.00	0.99–0.99	0.97–0.98	0.96–0.98
Yearling males ¹	0.95–1.00	0.97–1.00	0.91–0.94	0.90–0.92	0.85–0.90
Adult females ¹	0.98–0.99	0.98–0.98	0.99–0.99	0.98–0.98	0.96–0.97
Adult males ¹	0.93–0.95	0.96–0.97	0.91–0.93	0.90–0.92	0.85–0.89
<i>Annual</i>					
Calves not infested by winter tick	0.22–0.39	0.19–0.48	0.34–0.63	0.36–0.63	0.15–0.54
Calves infested by winter tick	0.00–0.40	0.00–0.47	0.00–0.62	0.00–0.66	0.15–0.48
Yearling females	0.95–1.00	0.94–1.00	0.88–0.95	0.85–0.94	0.79–0.90
Yearling males	0.90–1.00	0.91–1.00	0.83–0.91	0.78–0.88	0.70–0.82
Adult females	0.90–0.96	0.89–0.95	0.89–0.96	0.89–0.95	0.77–0.94
Adult males	0.86–0.94	0.87–0.95	0.79–0.91	0.75–0.88	0.70–0.85
Reproduction					
Parturition rate of yearling females	0.08–0.23	0.16–0.19	0.17–0.18	0.15–0.15	0.00–0.00
<i>after winter tick</i>	-	-	-	-	-
<i>after density dependence</i>	-	-	0.05–0.18	0.00–0.11	-
Parturition rate of adult females	0.73–0.92	0.65–0.87	0.68–0.89	0.64–0.86	0.49–0.77
<i>after density dependence</i>	-	-	0.68–0.88	0.56–0.79	0.44–0.76
Twinning rate	0.21–0.37	0.19–0.36	0.21–0.39	0.18–0.33	0.01–0.01
<i>after winter tick</i>	-	-	-	-	-
<i>after density dependence</i>	-	-	0.14–0.38	0.12–0.26	0.00–0.00
Immigration					
Yearling females (no. individuals/year)	0.05–0.87	0.90–1.13	4.42–4.78	6.74–9.72	6.87–7.57
Yearling males (no. individuals/year)	0.05–0.87	0.79–1.05	0.91–1.02	1.65–2.89	2.90–3.18
Adult females (no. individuals/year)	0.07–0.21	0.65–0.84	3.49–3.72	4.97–7.92	5.35–6.07
Adult males (no. individuals/year)	0.14–0.24	0.12–1.56	0.42–0.54	0.92–1.85	1.92–2.18
Proportion of yearling female immigrants ²	0.07–0.12	0.13–0.19	0.16–0.26	0.12–0.18	0.13–0.29
Proportion of yearling male immigrants ²	0.11–0.17	0.13–0.18	0.05–0.10	0.03–0.05	0.06–0.16
Proportion of adult female immigrants ²	0.00–0.01	0.01–0.01	0.03–0.04	0.02–0.02	0.01–0.02
Proportion of adult male immigrants ²	0.01–0.01	0.03–0.03	0.01–0.01	0.01–0.01	0.01–0.01
Emigration					
Yearling females (no. individuals/year)	1.01–3.28	0.57–1.57	1.52–3.45	0.00–11.6	3.99–11.5
Yearling males (no. individuals/year)	1.27–2.48	0.43–4.08	5.01–10.9	0.16–16.1	4.37–12.6
Adult females (no. individuals/year)	2.16–3.00	1.00–1.57	0.81–1.31	0.00–5.05	4.29–8.93
Adult males (no. individuals/year)	1.80–2.49	1.00–1.57	1.80–2.98	0.38–4.56	3.48–6.70

(continued on next page)

Table 4 (continued)

	Time period				
	1982–1989	1990–1996	1997–2008	2009–2016	2017–2019
Proportion of yearling female emigrants	0.14–0.44	0.06–0.18	0.06–0.09	0.00–0.16	0.13–0.20
Proportion of yearling male emigrants	0.19–0.33	0.04–0.40	0.22–0.30	0.01–0.22	0.14–0.22
Proportion of adult female emigrants	0.04–0.06	0.02–0.03	0.01–0.01	0.00–0.02	0.01–0.02
Proportion of adult male emigrants	0.07–0.09	0.02–0.03	0.03–0.03	0.00–0.03	0.02–0.03
Environmental parameters					
<i>Carrying capacity</i>					
Distance to carrying capacity (requirements/availability ratio) at the end of the time period	0.15–0.19	0.21–0.25	0.52–0.90	0.77–1.50	0.40–0.98
<i>Winter tick</i>					
Prevalence (% of infested moose)	0.00–70.0	0.00–70.0	0.00–70.0	0.00–70.0	10.0–70.0
Tick load (no. ticks/moose)	167–2320	202–2843	401–4426	608–5897	2623–6135
Years of “severe” infestation (>35,000 ticks/moose)	None	None	None	None	None

¹ The very narrow ranges of values for summer survival rates of yearlings and adults and autumn survival rates are due to the fact that they were not estimated with POM, but derived from field data (see Section 2.2.6).

² Calculated as the number of immigrants divided by the total number of individuals of this age- and sex-class in the Forillon National Park.

number of moose entering the park each year increased with time (Table 4). They were mainly females, with more yearlings than adults. Overall, the number of moose leaving the park each year also increased with time, except for a decrease in 2009–2016. Indeed, the scenarios with positive density dependence in dispersal were more supported than those with negative density dependence in dispersal, except for the period 2009–2016 (Table 3). Males were proportionately more numerous to emigrate than females.

4. Discussion

Our sex- and age-structured model, parameterized applying a pattern-oriented modelling strategy, successfully reproduced the observed dynamics of the moose population of the Forillon National Park over a 38-year period. It allowed us to identify one plausible picture of the evolution of the vital rates of this high-density population over time in a system without wolves and in a protected area free of hunting and logging, and to begin to disentangle the interactions between the different dynamics-driving factors and the associated biological mechanisms. Density-dependence seems to have played a key role in shaping the dynamics of this moose population through effects on survival, reproduction and dispersal, which is in line with our initial hypotheses. Winter climate also appeared to be an important factor that alternately interacted with moose density and winter tick load. However, contrary to our hypotheses, the effect of winter tick was probably restricted to winter calf survival, while the influence of predation and hunting may have been higher than expected. The relative importance of these factors varied over time, as winter climate and predation likely had a greater influence before 2000 (i.e. when moose density was relatively low), while density dependence became the leading factor afterwards.

4.1. Moose density as the major factor, impacting survival, reproduction and dispersal

According to the combination of vital rates identified by POM as the likeliest possibility among all supplied, the winter survival rates of calves were within the range of values generally observed (Ballard et al., 1991; Keech et al., 2011; Ausilio et al., 2023), although they were lower than could be expected in an area without wolves (e.g. Gasaway et al., 1983; Jolicoeur & Crête, 1988). The minimum value of 0.00 and maximum of 1.00 for the winter survival rate of calves infested by winter tick for the four first time periods were mainly due to very low tick prevalence (<1 %) for some simulations, leading to rounded numbers of calves dying. The winter survival rates of calves were more variable and sensitive to winter severity and population density than adult survival rates, as reviewed by Gaillard et al. (2000). These rates exhibited a

negative density dependence, which is consistent with the results of other studies in which a high population density was associated with higher mortality due to malnutrition (Clutton-Brock et al., 1991; Boertje et al., 2009). Winter survival rates of yearlings and adults appeared relatively buffered against variations in winter conditions. Indeed, in large herbivores, the adult survival rate is known to be more stable than the other vital rates, probably because individuals prioritize body maintenance over any other energy expenditure (Gaillard et al., 2000). However, winter survival rates of yearlings and adults decreased after 1996, particularly in 2017–2019. High-density populations are more sensitive to adverse climatic conditions because of decreased body condition (Coulson et al., 2001; Hansen et al., 2019), which could explain the low winter survival rates for all age classes between 2017 and 2019 when density was over 2.3 moose/km².

The reproductive rates of females were similarly high between the first three time periods. Considering the longer and snowier winters between 1990 and 1996, this suggests that when moose abundance is relatively low, reproductive rates can also be buffered against climatic variations, because females remain in good body condition, an observation documented by some studies (Gaillard et al., 2000; Desforages et al., 2021). However, when moose abundance was close to the carrying capacity (as in the 2009–2016 and 2017–2019 periods), our model suggested that the parturition rate of yearling females decreased to zero while the twinning and adult parturition rates were reduced. This could indicate that females prioritize survival and maintenance of body condition at the expense of reproduction. This is supported by findings made by other research teams (Sand et al., 1996; Gingras et al., 2014; Harris et al., 2021). Indeed, sufficiently restoring body fat reserves after calving at high population densities is more difficult due to increased food competition (Clutton-Brock and Coulson, 2002; Simard et al., 2010), so the probability of reproducing the next year may be reduced (Hamel et al., 2011).

Overall, emigration also increased with time, providing partial support to the hypothesis of a “positive density dependence in dispersal”, but decreased during the 2009–2016 period. This suggests that, as moose abundance reached carrying capacity, dispersal may have become less advantageous than philopatry. This could be explained by a decrease in body condition resulting from competition for food, decreasing the likelihood of dispersing (Hjeljord, 2001). Alternatively, the high density of females in the area could provide an enhanced access to mates for males of younger age classes and incite them to stay in the park (Røed et al., 2002; Loe et al., 2009). McFarlane et al. (2022) observed a negative density dependence in dispersal in a caribou population and hypothesized that it was due to the presence of remnant patches of high-quality habitat, coupled with an adverse effect of roads. Moreover, the park is considerably less disturbed than its surroundings

(e.g. no hunting, snowmobiling or logging), which makes it attractive for moose despite food competition.

All this evidence was consistent with moose having reached their carrying capacity (i.e. 2.3–4.5 moose/km² with a mean value of 3.3 moose/km²). This estimate is in line with the conclusions of Crête (1989), and with recent observations of similar moose densities in the neighbouring region of Bas-St-Laurent (Desgagnés et al., 2022). Our results did not allow us to decide on whether the moose forage in our study region is richer in metabolizable energy or nitrogen. Studies on other cervids (e.g. *Rangifer*: Barboza and Parker, 2008; Barboza et al., 2018) consistently reported that forage nitrogen is more limiting than energy, in particular during lactation. Parker et al. (2005) speculated that this might not be the case for all north-temperate cervids because the lichens consumed by reindeer and caribou in winter have a much higher energy/protein ratio than more commonly used forage species. Other authors reported more energy-limited (or balanced) diets in winter for several temperate ungulates (Hobbs et al., 1982; Parker et al., 1999). As for the summer season, digestible-energy-based estimates for the summer range carrying capacity for moose in Rocky Mountain National Park (Colorado) were 34 % lower than nitrogen-based estimates (Dungan et al., 2010), which is similar to our findings.

4.2. Predation as an important source of calf mortality due to high bear density

The proportion of calves killed annually by predators was high in our model (between 18 and 66 %) when compared to other studies conducted in areas free of wolves, where moose calf predation is usually < 30 % (Boer, 1987; Musante et al., 2010). However, such high values are not unique, as predation rates as high as 70 % were observed in caribou populations in the presence of black bears and coyotes (Lewis et al., 2017). This suggests that, despite the black bear being an opportunistic predator for moose, its relatively high density in the park may have resulted in a high calf mortality via a high encounter rate. Black bears are known to eat more animal prey in early summer, when moose calves are available, before shifting to a mostly plant-based diet later in the summer (Merkle et al., 2017; McLaren et al., 2021). Nevertheless, researchers have noted a great variation in bear diet between individuals, with some individuals “specialized” on mammal prey (Bastille-Rousseau et al., 2011; Edwards et al., 2011; Rioux et al., 2022). Coyotes may have accounted for a significant part of the calf mortality, although they are less abundant in the area than bears. Unfortunately, our model was not able to accurately partition the number of calves killed between these two predators. Indeed, when the black bear kill rate decreased, the associated calf mortality was automatically attributed to coyotes, with kill rates remaining within realistic ranges of values according to the literature. Thus, while predation rates were high at our population scale, the kill rates were low when compared to those observed in other studies for predation on young ungulates by black bears (Ballard, 1992; Rayl et al., 2018) and coyotes (Benson et al., 2017). In addition, implementing a maximum value for the predation rate made us unable to confirm or reject our hypothesis of a slight decline in coyote density after 2015, because (1) a small change in the coyote density no longer influenced the proportion of dying calves, and (2) as mentioned above, the mortality caused by coyotes could not be distinguished from that due to bears.

4.3. Winter conditions influence vital rates differently over time

Different scenarios were highlighted depending on the time period, indicating that the way in which winter conditions influenced the vital rates likely changed over time, with potential evidence of a carryover effect. Our model clearly selected a 1-year lag in the effect of winter conditions on reproductive rates for the 1982–1989, 1990–1996 and 2009–2016 periods. Several studies conducted on ungulates found such a negative correlation between female fecundity and snow accumulation

or persistence in the winter preceding gestation (Mech et al., 1987; Post and Stenseth, 1999; Garroway and Broders, 2007). The associated biological mechanism would be the difficulty of females to sufficiently restore their body fat reserves during summer (especially if they are lactating), redirecting the resources to self-maintenance and inducing a reproductive pause (Clutton-Brock et al., 1989; Parker et al., 2009). Such a mechanism could have been at play for the 1990–1996 period when winters were relatively snowy, and the snow melted relatively late. However, for 2009–2016, when winters were milder, the capacity of females to reach a body condition sufficient for gestation could have been constrained by intraspecific competition, considering the very high moose densities. In contrast, in 1997–2008 and 2017–2019, the selected scenarios suggested no carryover effect of winter on reproduction, which could appear counter-intuitive regarding the very snowy and long winters of 2017, 2018 and 2019. However, scenarios with a carryover effect of winter conditions on winter calf survival were strongly selected for this time period, suggesting that instead of impacting the ability of females to conceive, severe winter conditions during gestation led to lighter or weaker newborns, which were less likely to survive their first winter. This phenomenon was described in several studies (Adams, 2005; Lamb et al., 2023).

4.4. Limited effect of winter tick on population dynamics suggests low tick load in the area

The simulations for which the mean values and confidence intervals for the three patterns fell into the confidence intervals of the aerial surveys steadily displayed low mean tick loads. This is consistent with the findings of several authors; at high latitudes, in areas where winters are long (i.e. shorter seasons for questing larvae and decreased probability of egg-laying for adult female ticks), moose tick load is limited by climate and expected to be low, unless moose densities become high (> 1 moose/km²; Samuel, 2007; Dunfey-Ball, 2017). Nevertheless, we believe that our estimates are biased downward, since it is unlikely that a tick load of only 2500–6000 ticks/individual caused such a difference in winter survival rate between infested and non-infested calves in 2017–2019. We conclude that our model was more efficient at estimating the effect of tick infestation on moose vital rates than the winter tick load itself. Our results also suggest that there was only little or no difference between the survival rates of infested and non-infested calves, except in the 2017–2019 period (although the ranges of values largely overlap). This slight difference is supported by recent observations made by a research team that compared the survival rates of moose calves treated vs. untreated with acaricides in different regions of Quebec (V. Bonin-Palardy, *unpublished data*). They noted that Forillon National Park was among the regions with the smallest differences between the survival rates of treated and untreated calves. The higher disparity in survival between infested and non-infested calves for the 2017–2019 period can reflect an interaction between tick load and winter climate or density. Indeed, tick-induced self-grooming, hair damage and blood loss can cause a decrease in body condition of infested calves, and make them more sensitive to density effects or severe winter conditions, as was documented in several studies (Samuel, 2004; Musante et al., 2007; Ellingwood et al., 2019).

4.5. Sex-biased dispersal and hunting shape moose sex ratio

Our model used different dispersal rates between males and females to explain the variations in moose sex ratio between time periods. According to our model, males were more susceptible to disperse in all periods. This is in accordance with the mating strategy typically observed in mammals, where local mate competition, inbreeding avoidance and female mate choice often lead to a male-biased dispersal (Greenwood, 1980; Lawson Handley and Perrin, 2007). Our model also suggested that immigration was mainly composed of females, a finding consistent with the fact that females constituted the major part of the

population outside the park: indeed, moose sex ratio in the hunting zone n°1 fell from 0.53 in 2000 to 0.20 in 2017 (Landry and Lavergne, 2007; Dorais and Lavergne, 2017). Females may have used the park as a “refuge” from hunting or other human disturbances, as was observed in other studies (Coppes et al., 2017; Sergeyev et al., 2022). Moreover, as moose density increased, hunting around the park likely further contributed to this bias in sex ratio, as it removed 11–15 % of the males annually from 2017 to 2019.

4.6. Limitations and potential research avenues

Having to fix the values of 63 parameters to meet the conditions for use of the POM method may appear as an obvious limit of our study, as it may have constrained the model from exploring combinations of parameter values that include values near the extremes of the ranges. However, fixing 63 parameter values substantially improved the success rates for all time periods (see Supplementary Material 9), and our results with 83 unfixed parameters (Supplementary Material 5) were generally similar to those with 20 unfixed parameters. The exception to this would be the tick load, which displayed higher variability with 83 unfixed parameters and even crossed the line of “severe infestation” for several years in some rare cases (see Supplementary Material 5). It may thus be valuable to explore more quantitatively under which conditions and with which gain the POM method can be used to estimate more than 20 parameters at a time.

One could still argue that we used POM to first estimate 63 parameter values before using it a second time with the remaining 20 variables. However, we consider it a relevant exploratory phase that allowed us to confirm (1) which parameters could be fixed without overly reducing the model’s explanatory capacity, and (2) the values to be used, instead of fixing them arbitrarily. While a much simpler model could certainly reproduce all the data, building a model with the smallest number of parameters was not our goal, since we wanted to be able to answer wildlife managers’ questions about the relative influence of various factors known to potentially impact moose demographics, while providing a platform that could potentially be (adjusted for and) applied to other study areas, other populations and other population levels, in which the hierarchy of factors determining demography (and their relative importance) could be modulated. Not knowing at the outset which parameters would have the most influence, the best approach to building a model that could meet our objectives was therefore to work on a more complex model.

Using the POM method with patterns of a single hierarchical level was not an ideal situation and probably decreased the level of precision of our model (Grimm and Railsback, 2012). Nevertheless, we are confident that our model achieved a certain structural realism as some properties of real systems that were not explicitly coded for still arose from it, such as the most important parameters for each pattern disclosed by our sensitivity analysis (see also the Supplementary Material 10 for a picture of the closeness between simulated and observed patterns). Another shortcoming of scarce data was that the parameter ranges to be explored were so wide that POM could always find an adequate combination to reproduce the observed patterns regardless of the value of certain parameters (see Supplementary Material 11). This is the case of winter tick prevalence and winter tick load, whose values in successful simulations covered wide ranges of possible values for all time periods. This demonstrates the limited capacity of our model to estimate them. As mentioned above, this consideration may also be true for the kill rates of black bears and coyotes (which were used interchangeably by the model to kill a given proportion of calves), and to a certain extent for moose carrying capacity in the park (when taking into account the uncertainties around the values derived from the surveys, the observed moose abundance in 2017 could be reproduced with winter carrying capacities ranging from 2.3 to 5 moose/km²; see also Supplementary Material 12). Investigating how the kill rates vary with the relative densities of black bears, coyotes and moose would be useful for

wildlife managers in such areas and for future model builders. In addition, these new data would constitute a strong supplementary pattern on the community level that could perhaps be integrated to our POM approach to improve the accuracy of our model.

Moreover, we were not able to validate some vital rates or parameters derived from our model with another dataset from a companion study. What can be considered as a first step of this validation process is a study in which the field sampling took place in Forillon National Park from winter 2023 to winter 2024 (M. Ouellet, *unpublished data*). This study was designed to investigate the causes of the recent low moose recruitment rates in the park. The percentage of pregnant females in winter 2023 was estimated to be around 85 % (through progesterone dosing in pellets), with an effective parturition rate of 80 % (determined by tracking changes in female movement patterns) and a twinning rate of 25 % the following spring (direct visual count). In addition, capture-mark-recapture models yielded a cumulative 10-month survival rate of 39 % for calves (M. Ouellet, *unpublished data*). This last value falls into our range of estimated values for the annual calf survival rate for the 2017–2019 period, although Ouellet’s (*unpublished data*) estimated parturition and twinning rates are higher than our maximum values. These differences may be associated to a parametrization covering a wider period of time in our model compared to this companion study, with potential slight variations of vital rates (such as emigration and calf survival). Furthermore, the values of reproductive rates might not be the same in 2023 as in 2017–2019, especially considering the fast decrease in moose density that happened over these years.

Finally, the validity of our results assumes that the data obtained via aerial surveys (and used as patterns to parameterize our model) are accurate. However, variations in the methods and timing of monitoring between the time periods may have caused a bias in some estimates (see Supplementary Material 1). Furthermore, a recent study pointed out that the aerial inventory standards used since the 90s for moose in Quebec do have some weaknesses that might compromise the precision of density estimates (Gagnon-Labrosse, 2022). Some of these weaknesses were corrected in the park’s sampling protocols, so that the values derived from the surveys still provide useful orders of size for modelling.

4.7. Contributions

Our work led to a new estimated range of values for the moose carrying capacity in Gaspésie, and presented a global picture of the evolution of a moose population’s many vital rates over time and how they articulate with each other, whereas a lot of studies only focused on survival/mortality, reproduction or dispersal. Some structural refinements may be needed to improve the hindcasting capacity of our model. This could be achieved as a next step of this project by, for example, starting with a simpler, basic model and progressively testing hypotheses to add complexity, comparing the new obtained model structure to the present one and confronting them to supplementary datasets. This would help discover if other causal factors, or different ways of modelling the same factors, would lead to different ranges of possibilities. In this regard, our work helped target which data type would be the most useful to gather. Our study also describes the shortcomings of the POM method and highlights the new opportunities it presents when applied to a model with many parameters to calibrate while using limited field data. Despite some remaining uncertainties, our approach allowed us to identify a plausible sequence of vital rates, along with their drivers and the interactions between them, with little baseline data.

CRedit authorship contribution statement

Louana Tassi: Writing – original draft, Validation, Software, Methodology, Investigation, Formal analysis. **Pierre Etcheverry:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Sarah Bauduin:** Writing –

review & editing, Software, Methodology. **Martin-Hugues St-Laurent:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare no competing interests that could have influenced this work.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.ecolmodel.2026.111528](https://doi.org/10.1016/j.ecolmodel.2026.111528).

Data Availability

Data and R scripts supporting this work are available on Dryad at DOI: [10.5061/dryad.mpg4f4rdj](https://doi.org/10.5061/dryad.mpg4f4rdj).

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